Modeling in-situ pine root decomposition using data from a 60-year chronosequence

Kim H. Ludovici, Stanley J. Zarnoch, and Daniel D. Richter

Abstract: Because the root system of a mature pine tree typically accounts for 20–30% of the total tree biomass, decomposition of large lateral roots and taproots following forest harvest and re-establishment potentially impact nutrient supply and carbon sequestration in pine systems over several decades. If the relationship between stump diameter and decomposition of taproot and lateral root material, i.e., wood and bark, can be quantified, a better understanding of rates and patterns of sequestration and nutrient release can also be developed. This study estimated decomposition rates from in-situ root systems using a chronosequence approach. Nine stands of 55- to 70-year-old loblolly pine (*Pinus taeda* L.) that had been clear-cut 0, 5, 10, 20, 25, 35, 45, 55, and 60 years ago were identified on well-drained Piedmont soils. Taproot and lateral root systems were excavated, measured, and weighed. Although more than 50% of the total root mass decomposed during the first 10 years after harvest, field excavations recovered portions of large lateral roots (>5 cm diameter) and taproots that persisted for more than 35 and 60 years, respectively. Results indicate that decomposition of total root biomass, and its component parts, from mature, clear-cut loblolly pine stands, can be modeled with good precision as a function of groundline stump diameter and years since harvest.

Résumé : Étant donné que le système racinaire d'un pin mature représente normalement 20–30 % de la biomasse totale de l'arbre, la décomposition de la racine pivotante et des grosses racines latérales, à la suite d'une récolte et de la régénération du peuplement, pourrait avoir un impact sur la disponibilité des nutriments et la séquestration du carbone dans les pinèdes pendant plusieurs décades. Si la relation entre le diamètre de la souche et la décomposition des constituants de la racine pivotante et des racines latérales, i.e. le bois et l'écorce, peut être quantifiée, il serait possible d'avoir une meilleure compréhension des taux et des patrons de séquestration et de mise en disponibilité des nutriments. Cette étude a estimé le taux de décomposition de systèmes racinaires in situ en utilisant une approche chronoséquentielle. Neuf peuplements de pin à encens (*Pinus taeda* L.) âgés de 55–70 ans coupés à blanc il y a 0, 5, 10, 20, 25, 35, 45, 55 et 60 ans ont été identifiés sur des sols bien drainés du Piedmont. La racine pivotante et les racines latérales ont été déterrées, mesurées et pesées. Bien que plus de 50 % de la masse totale de racines ait été décomposée au cours des 10 premières années suivant la récolte, les travaux d'excavation ont permis de récupérer des portions de grosse racine latérale (diamètre > 5 cm) et de racine pivotante qui persistaient après plus de 35 et 60 ans respectivement. Les résultats indiquent que la décomposition de la biomasse racinaire totale et de ses composantes, dans les peuplements matures de pin à encens coupés à blanc, peut être modélisée avec une bonne précision en fonction du diamètre de la souche au niveau du sol et du nombre d'années écoulées depuis la récolte.

[Traduit par la Rédaction]

Introduction

The uptake of soil nutrients and water by tree roots and the subsequent release of nutrients through decomposition are important processes contributing to long-term forest productivity. Roots are the principle source of organic matter in the deeper soil layers, and their decomposition rates impact release rates of forest soil nutrients. Estimates of organic matter inputs and turnover in soil are based in part on assumptions that are not well quantified. The mean annual increase in the mass of the feeding roots in many forests, for example, are estimated to be equal to the quantity of feeding roots that die off (Cox et al. 1978; Joslin and Henderson 1987; Raich and Nadelhoffer 1989; Nadelhoffer and Raich 1992). However, decomposition dynamics of larger roots are likely to be much different from fine roots and are almost entirely unquantified. Because root dynamics control rates of nutrient release to soil pools, current estimates of site resource requirements for sustaining forest productivity have considerable uncertainty. Increased understanding of large root decomposition would enhance the ability to predict nutrient and carbon cycles in the forest ecosystem and contribute to a better understanding of site productivity.

A mature pine tree root system typically accounts for 20–30% of the total tree biomass (Wells et al. 1975; Pehl et al. 1984; Van Lear et al. 2000). Large primary lateral roots are commonly the same or similar in age to the tree itself (Vogt and Persson 1988) and represent a large pool of stored resources. Studies of fine roots of several tree species indicate

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that decomposition rate decreases as a function of increasing root diameter (Fahey et al. 1988; King et al. 1997; Chen et al. 2001). Thus, decomposition of large lateral roots and taproots can potentially impact nutrient release over several decades (Olsen 1963; Jenny 1980; Vogt et al. 1991; Chen et al. 2001). The frequency and temporal dynamics of this input are dependent of tree mortality and site disturbance.

Loblolly pine (*Pinus taeda* L.) occupies 21×10^6 ha of forestland in the southeastern United States and accounts for 56% of all planted tree acres in the region (USDA 2000). Sustainability of this forest resource is of increasing importance as land-use patterns change and intensity of management increases site productivity. Most forest soils in the U.S. Southeast have low native fertility. Previous agricultural land uses have greatly altered soil nutrient status and eroded many of the region's clayey soils. The Georgeville series represents 8% of the total land base in the Piedmont and nearly 25% of forested lands in the region. These, and related soils, have relatively small contents of soil organic matter, and nutrient availability is likely to be highly dependent on the turnover and decomposition of large-root systems (Van Lear et al. 2000).

The objective of this study was to quantify decomposition rates of large lateral roots and taproots in situ, over time scales of decades. In this study, management records of the Duke Forest in central North Carolina were used to identify old-field loblolly pine stands that had been clear-cut over a 60-year period (1939–2000). Nine stands of natural regeneration pine, supported by Georgeville series soils, were identified to locate loblolly pine stumps that were subject to decomposition for up to 60 years. A model was developed to predict the mass of lateral and taproots as a function of stump diameter and time since harvest. Decomposition rates for various root components were obtained from parameters of the models.

Materials and methods

Study sites

A chronosequence of nine clear-cut stands of old-field loblolly pine (55–70 years old) was identified at the Duke Forest, Durham County, North Carolina. This type of harvest and sequence of stand ages represent an important condition for carbon loading and decomposition on the Piedmont upland landscape (Richter and Markewitz 2001). Stands were selected for uniformity in soil series, species, landform, regeneration, land management, and current overstory. Management records and ground truthing revealed that the stands were clear-cut 5, 10, 20, 25, 35, 45, 55, and 60 years ago. One 55-year-old, intact stand was also selected for comparison and three live trees felled. Most were in the Korstian Division of the Duke Forest, near the intersection of Mount Sinai Road with Turkey Farm Road. Soils were of the Georgeville series with very deep, well-drained, moderately permeable soil that has formed in material weathered from Carolina slate (fine, kaolinitic, thermic Typic Kanhapludults). Slopes ranged from 2 to 10%, and the current stand vegetation is predominantly naturally regenerated loblolly pine of 0–60 years of age. Annual precipitation averages about 123 cm, mean annual temperature is 16°C, and the frost-free season ranges from 190 to 240 days (Albaugh et al. 1998).

Sample collection and measurements

In June 2000, three tree stumps were randomly selected in each of the nine stands and excavated to recover large lateral roots within 1 m of the stump edge, and taproots within 1 m of the soil surface (Fig. 1). Two additional decomposing root systems that had grafted lateral roots were excluded because grafting allows root systems to continue to live after harvest. Three live trees were selected for representative size and were felled to serve as time 0. Roots were separated into consolidated solid and unconsolidated soft decomposing taproot material, and lateral roots by depths of 0–50 and 50–100 cm. Bark was composited from the taproots and lateral roots. All samples were transported to the USDA Forestry Sciences Laboratory in Research Triangle Park, N.C.

After a tree stump was identified, the forest floor was cleared within a 1-m distance from stump circumference, and all aboveground material was removed. Diameter at ground level was measured at two points inside the bark and averaged. In stands harvested at 0, 5, and 10 years in the past, a ditch witch was used to severe lateral roots 1 m away from the tree stumps. All taproots were excavated to a depth of 1 m and the diameter at the bottom of the root hole, or at the taproot fork, was recorded. Picks, shovels, and scrapers were used to remove soil from crevices and exteriors of each intact stump. Diameter and length of each taproot was measured to estimate total root volume. Slices of solid taproot tissues were collected to estimate root density. Root systems from plots harvested within the previous 15 years required a backhoe for complete excavation. Those harvested 20 and 25 years in the past were extracted with the aid of a heavy-duty winch, and all others were hand excavated. Taproots from 12 of the 27 stumps extended deeper than 1 m, and that mass was also excavated (mean 6.6 kg) but was not included in the model.

Lateral roots were located by hand excavation around each stump and were carefully unearthed to a 1 m distance from stump circumference. Diameter was measured for each lateral where it originated along the taproot surface. Stumps were first excavated to a depth of 0.5 m, ensuring that all laterals were measured and noted for depth of origination (at 0–20 or 20–50 cm soil depth), and then excavated from the full 1 m depth. Finally, lateral root and bark materials were recovered from root channels to a maximum distance of 1 m from the stump edge. All root material was oven-dried to a constant mass at 65°C and weighed. Every sample was chipped, ground, and had loss on ignition performed to correct total biomass calculations for mineral soil contamination. Soil contamination was more evident in lateral root samples than in taproot samples, as lateral root diameters were small and even careful hand excavation often disturbed root channels less than 5 cm. Soil contamination was rarely problematic in decomposed taproot samples, as soil compaction around the taproot was so extreme as to withstand hand shovels and determined removal of bark from the root hole.

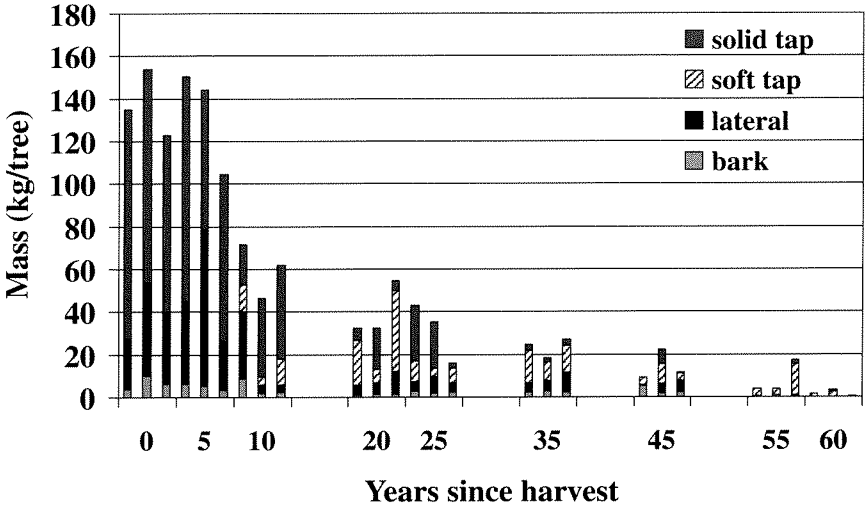
Statistical analysis

Initially an exponential function was used to estimate the decomposition rate of root materials (Yavitt and Fahey 1982; Bloomfield et al. 1993). It was defined as

$$[1] \qquad \mathrm{WT}_t = a\, \mathrm{e}^{-c(\mathrm{YSH})}$$

Fig. 1. Photograph of recovered root material from 55- to 70-year-old loblolly pine stumps that had been decomposing for (A) 5 years, (B) 20 years, (C) 10 years, and (D) 55 years on a Kanhapludult in the Piedmont region of North Carolina.

Fig. 2. Actual biomass of each component of recovered loblolly pine root systems, Durham, N.C., June 2000.



where WT_t is the mass remaining at time t, a is the initial mass, c is the decomposition rate, and YSH is years since harvest. This model assumes that decomposition is proportional to the amount of material remaining. The utility of this model is that root mass could be predicted merely as a function of years since harvest. The exponential function was then modified to allow the intercept and decomposition rate to be linear functions of stump diameter, yielding

$$[2] \qquad WT_t = [a + b(\mathrm{DIAM})]e^{-[c+d(\mathrm{DIAM})]\mathrm{YSH}}$$

where DIAM is the average stump diameter and a, b, c, and d are parameters to be estimated. It was hypothesized that predictability of root mass would be increased if information on stump diameter was included. To investigate the effect of soil depth, models were fit to data from the 0–50 cm depth and the 50–100 cm depth separately.

These nonlinear models were fit using the PROC NLIN procedure with the GAUSS option (SAS Institute Inc. 1985). Separate mass models were fit to the lateral root wood, soft taproot wood, solid taproot wood, total taproot wood, bark component, and total roots (lateral, total tap, and bark combined). The models were evaluated based on the mean square error (MSE) criterion and the correlation of the observed with the predicted. The residuals were examined by plotting them over the predicted and dependent variables for each model.

Half width of the confidence interval on the predicted mean was also used as a criterion for predictability. The criteria used to evaluated this was the absolute error defined as

$$[3] \qquad \mathrm{AE} = \frac{\hat{Y}_\mathrm{U} - \hat{Y}_\mathrm{L}}{2}$$

and the percent error defined as

$$[4] \qquad \mathrm{PE} = 100\frac{(\hat{Y}_\mathrm{U} - \hat{Y}_\mathrm{L})/2}{\hat{Y}}$$

where $\hat{Y}$ is the predicted mean from the regression model, $\hat{Y}_\mathrm{L}$ is the lower 95% confidence interval limit on the predicted mean, and $\hat{Y}_\mathrm{U}$ is the upper 95% confidence interval limit on the predicted mean

The absolute error is the half width of the 95% confidence interval on the predicted mean and the percent error is the absolute error expressed as a percent of the predicted mean. As variability of the predicted mean increases, the width of the confidence interval increases and, consequently, these two criteria become larger.

The total root mass consists of the lateral wood, tap wood and bark mass components, and thus, this set of models could be considered a system of nonlinear, dependent equations. Parresol (2001) presented methods to fit such a system that has the property of additivity of components. However, in our research it was desired to obtain the best equations for each component without imposing restrictions for additivity.

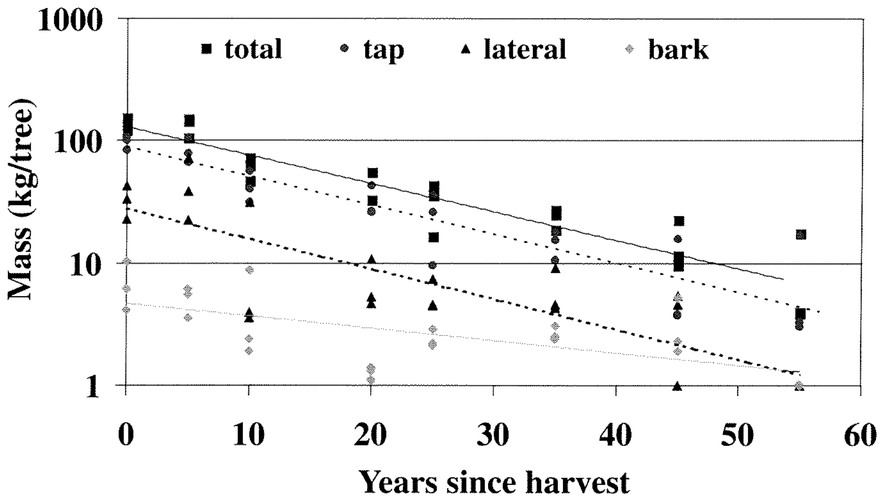
Results

Root biomass

The absolute amount of each root component decreased with time since harvest, and total root mass had decreased by more than 50% at 10 YSH (Fig. 2). On average, taproots contributed 71% of the root mass excavated within 1 m of a stump, while lateral roots contributed 25% (Fig. 2). Solid taproot mass decreased approximately 15% during the first 5 years and approximately 65% during the first 10 years, had almost 20% remaining after 25 years, and was still measurable at 60 YSH. Soft taproot tissue was recovered from stumps decomposing 10 years or more. The percentage of root mass composed of decomposing or soft taproot tissue increased with time, but these data were variable. The mass of soft taproot tissue increased through 20 years post-harvest and then decreased (Fig. 2). Lateral roots contributed between 17 and 30% of the excavated root mass, with a mean of 40% of all lateral root mass remaining 10 years after harvest and small but measurable quantities recoverable at 60 years. Contribution of bark to large root mass ranged from 3 to 24%, increasing through the first 45 years before declining sharply thereafter.

The pattern of increasing bark percentage contributions to total remaining mass, with the percent taproot and lateral root contribution remaining relatively constant indicates different rates of decomposition for the taproot wood, lateral

Fig. 3. Actual biomass of recovered loblolly pine root components expressed on a log scale to quantify decomposition rates, Durham, N.C., 2000.



root wood, and bark tissues. To quantify this, individual root component mass was displayed on a log scale (Fig. 3) and decomposition rates (k) were estimated (Table 1). Decomposition rates were –0.055 for taproot wood, –0.057 for lateral root wood material, and –0.053 for the root system in total. Decomposition rates for bark (–0.023) were less than one-half of other root tissues.

Table 1. Decomposition rates (k) of each mature loblolly pine root component, Durham, N.C., June 2000.

Root component	Intercept	k	R^2
Total taproot	89.536	0.0546	0.81
Lateral root	27.867	0.0568	0.71
Root bark	4.680	0.0233	0.40
Total root	129.600	0.0534	0.86

Modeling of root biomass

Prediction equations of remaining total large root mass lose robustness by 20 years since harvest, as indicated by increasing percent errors around the predicted mean (Fig. 4A). This deviation from actual values is an indication of differences between lateral root and taproot material, as individual components of taproots and lateral roots decreased at different rates. Decomposition model parameters and fit statistics for individual root components and several component combinations are shown in Table 2. Regression analyses to predict biomass of different combinations of root material (Fig. 5) were compared with results from regression analyses of the total large root model. The weakest relationship was for soft taproot wood mass, which had a MSE of 59.9 and a correlation coefficient of 0.53 (Table 2). Regression analysis of the solid taproot wood was not different from that for the combined solid and soft taproot measure.

Fitting a system of nonlinear equations using PROC SYSNLIN confirmed that no additional improvement in the total root model was achieved compared with individual component models. The relationship between total root biomass, time in YSH, and stump diameter was the strongest with MSE of 202.9 and a correlation coefficient of 0.96 (Table 2).

Strength of the models is displayed in the graphs of predicted against actual biomass values. The variability of these relationships is depicted in Figs. 6A–6C, with actual masses of individual root components, bark, lateral wood, soft wood, and solid taproot wood plotted against their predicted values. Evaluation of predicted stump masses against actual masses supported the strength of the models for total root mass (Fig. 6A), total taproot mass (Fig. 6B) and solid taproot mass (Fig. 6B), as correlation coefficients (r) were greater than 90% for each (Table 2). Soft taproot tissue mass was unrelated to YSH and stump diameter (Fig. 6B). The ability to predict lateral root mass was adequate with an r of 0.756 (Fig. 6C). Bark mass was significantly described by the model but could only be adequately predicted by these models at the 75% confidence level (Fig. 6C). Predictability of solid taproot wood through time was strong with an r of 0.916 and a probability of <0.0001, and combining both soft and solid taproot wood components altered the equation for biomass prediction, without changing its strength (Table 2).

Inclusion of depth, as a factor in decomposition, suggested that individual root components at different depths decompose at different rates. The ability to predict total, solid taproot wood mass, or a combined solid and soft taproot wood mass within a depth decreased with increasing depth (Table 3). Strength of the relationship between stump diameter, YSH, and remaining mass was strongest for total stump, total taproot wood, and soft taproot wood, in the 0–50 cm depth, and strongest for total stump, total taproot wood, and lateral root mass prediction in the 50–100 cm depth (Table 3).

Prediction evaluation

An evaluation of the models to predict biomass components was based on a measure of precision obtained from confidence intervals constructed on the predicted mean value. Percent errors were defined as the half width of 95%

Fig. 4. (A) Percent error of the predicted mean using the regression model for root component decomposition and (B) the absolute error is the half width of the 95% confidence interval on the predicted mean, Durham, N.C., 2000.

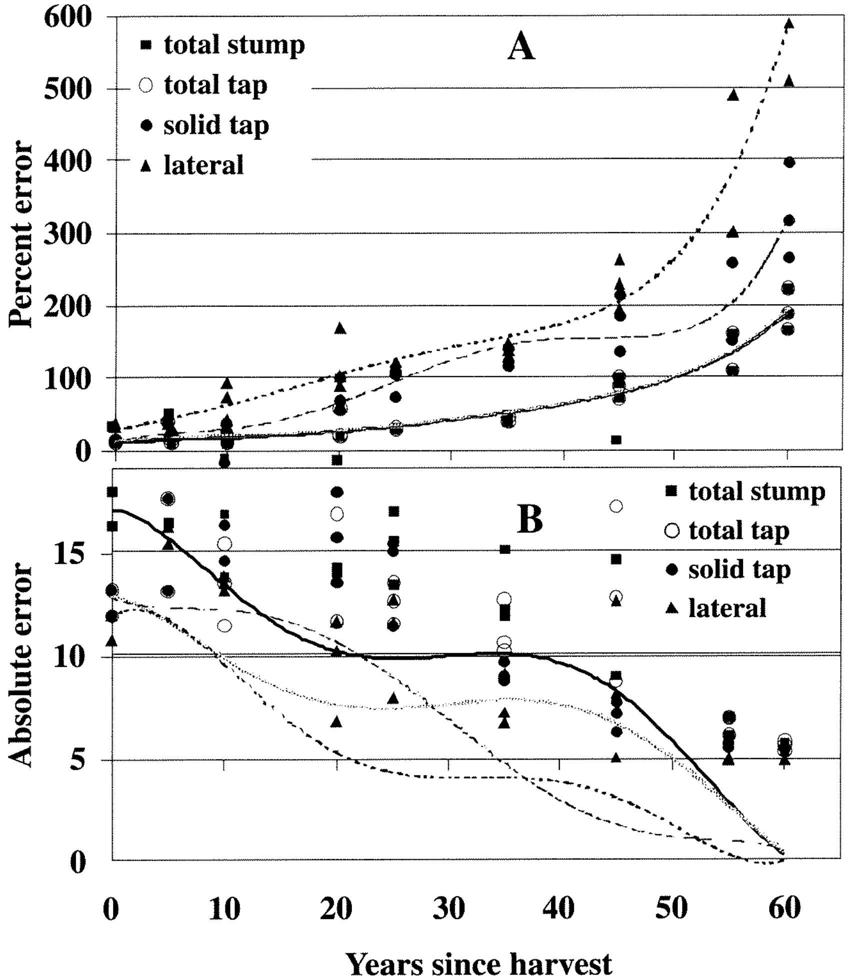
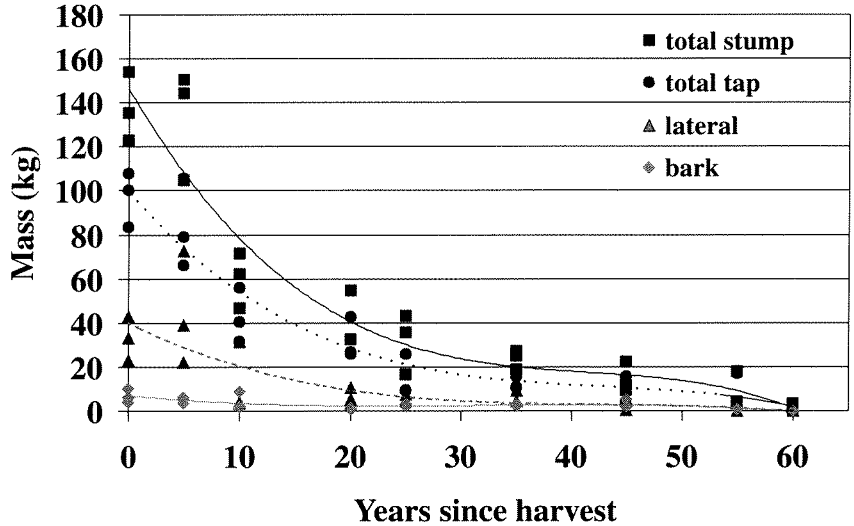


Table 2. Parameters and fit statistics for the initial exponential model 1 and the modified model 2 that allows the intercept and decomposition rate to be linear functions of stump diameter.

Root component	Sample size	Model[a]	a^b	b	c	d	MSE[c]	r^d
Lateral root	24	1	39.3*	—	0.0677*	—	149.4	0.75
		2	–27.4	1.44	0.4079	–0.0052	101.6	0.86
Soft taproot	21	1	17.7*	—	0.0198	—	61.8	0.42
		2	–21.2	0.72	–0.0140	0.0006	59.9	0.53
Solid taproot	24	1	103.3*	—	0.0880*	—	156.4	0.95
		2	44.6	1.30	0.1046	–0.0000	147.9	0.95
Total taproot	27	1	98.8*	—	0.0589*	—	120.7	0.95
		2	103.6*	–0.11	0.1467*	–0.0016	116.1	0.96
Root bark	27	1	6.3*	—	0.0361	—	3.5	0.71
		2	10.8*	–0.10	0.1194	–0.0016	3.4	0.75
Total root	27	1	144.9*	—	0.0600*	—	263.9	0.95
		2	89.4*	1.16	0.1502*	–0.0015	202.9	0.96

[a]Model 1 is $WT = a\,e^{-c(YSH)}$ and model 2 is $WT = (a + b\mathrm{DIAM})e^{-(c+d(\mathrm{DIAM}))YSH}$.
[b]An asterisk indicates that the parameter is significantly different from zero at the 0.95 probability level.
[c]The mean square error from the nonlinear regression fit.
[d]The correlation coefficient between the observed and predicted.

Fig. 5. Biomass of mature loblolly pine root systems recovered along a time chronosequence, with fitted equations for regression of each root component against time and stump diameter, Durham, N.C., 2000.



confidence intervals and presented as a percentage of the predicted mean (Fig. 4A). In general, error remained less than 20% through 10 YSH for total stump and total taproot wood components and was less than 30% through 25 YSH. Although percent errors generally increased with increasing YSH, absolute values decreased (Fig. 4B). The equation of total stump mass (Fig. 7) produced the smallest percent error, ranging from 10 to 221% (Fig. 4A). Percent error ranged from 10 to 58% for the first 35 years post-harvest, increasing to values of 100% after 55 years, and 200% after 60 years. This error around the predicted mean of total mass appears large on a percentage basis; however, absolute error ranged from 0.0 to 1.4 kg at 55 and 60 YSH.

Discussion and conclusions

Loblolly pine root systems persist for a long time on southern sites. Stump holes and lateral root channels could be easily identified even 60 YSH, as we observed that soil compaction around the root systems was obvious and long lasting. Root systems thus provided multiple long-term benefits to the site. Before 10 YSH, a developing space between decomposing roots and the mineral soil matrix, created a favorable environment for new elongating roots (Van Lear et al. 2000). The high water content of decomposing roots was obvious when water spurted from the 5 YSH roots as they were excavated. Van Lear et al. (2000) demonstrated that after 10 YSH, established root channels provided a favorable rooting environment for growth of new roots. In that study, fine roots proliferated through old root channels where resources were concentrated and impedance was minimal. The established root channels likewise created favorable environments for insects, herpetofauna, and small mammals.

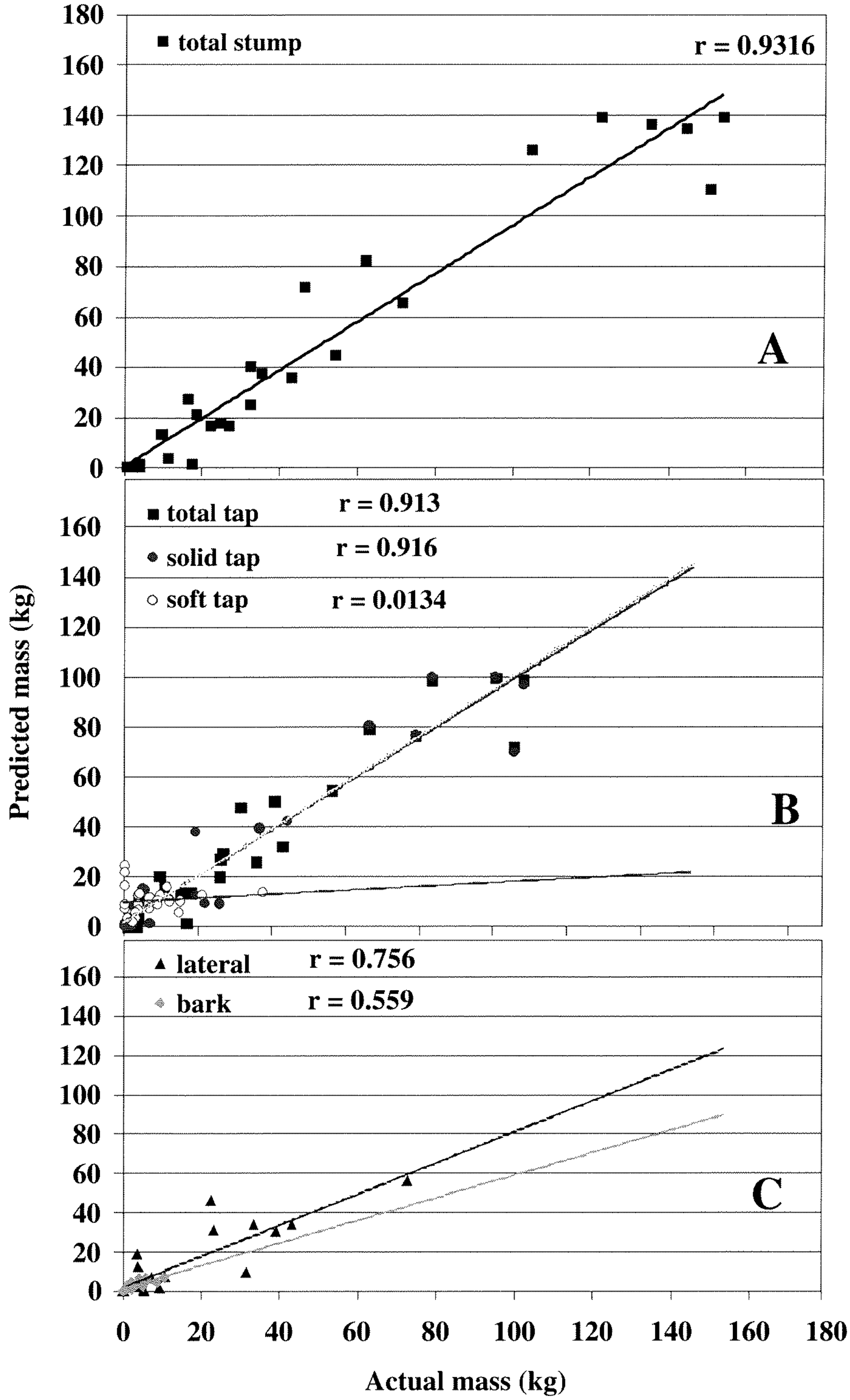
On average, taproots of these mature pines initially contributed 71% of the excavated root mass, while the lateral roots contributed 25%. This distribution is somewhat different from the taproot contributions of 50–55% and lateral root contributions ranging from 21 to 45%, reported for younger pine trees (Wells et al. 1975; Harris et al. 1977; Van Lear and Kapeluck 1995). Such differences in distribution could be expected because of the different soil volumes explored by trees of different ages. A young tree is likely to distribute the majority of belowground biomass near the surface and within a 1-m distance from the stem. A mature pine tree is expected to have a taproot longer than 120 cm, with lateral roots extending beyond the canopy. As a tree ages, we would expect increasing proportions of the total root biomass to be taproot wood, when excavation is confined to a 1-m distance of the stem.

The pattern of decreasing lateral-root and increasing bark contributions, while relative taproot contribution remained similar through time, indicated different rates of decomposition for the taproot wood, lateral root wood, and bark tissues. The calculated decomposition rate for bark (0.023) was less than one-half the rate for lateral root wood (0.057) or taproot wood (0.055).

Individual root components decompose at different rates at different depths. We expected that these clear-cut sites would have high rates of decomposition because temperature and soil water availability were high and microbial populations were clustered at existing root sites. Our decomposition rates were generally faster than those reported by Chen et al. (2001) for western tree species on northwestern U.S. locations. Comparison of decomposition rates for different species and in different latitudes indicates that (with the exception of lodgepole pine, (Chen et al. 2001)) loblolly pine roots decompose at faster rates.

The ability to quantify belowground biomass is critical to our ability to model carbon fluxes in forests. Yavitt and Fahey (1982) suggested that decomposition of sapwood and heartwood of woody roots should be examined separately to allow more accurate estimation of long-term root mass loss. Chen et al. (2001) also reported that a double-exponential model, which accounts for sapwood and heartwood components separately, provides a better fit than the single-exponential model for woody roots. However, our study did not confirm the need to evaluate various structural components separately in estimating long-term decomposition.

Fig. 6. Predicted and actual mass data for recovered decomposing pine root systems (A) total stump mass, (B) taproot wood components, and (C) lateral wood and bark tissues, Durham, N.C., 2000.



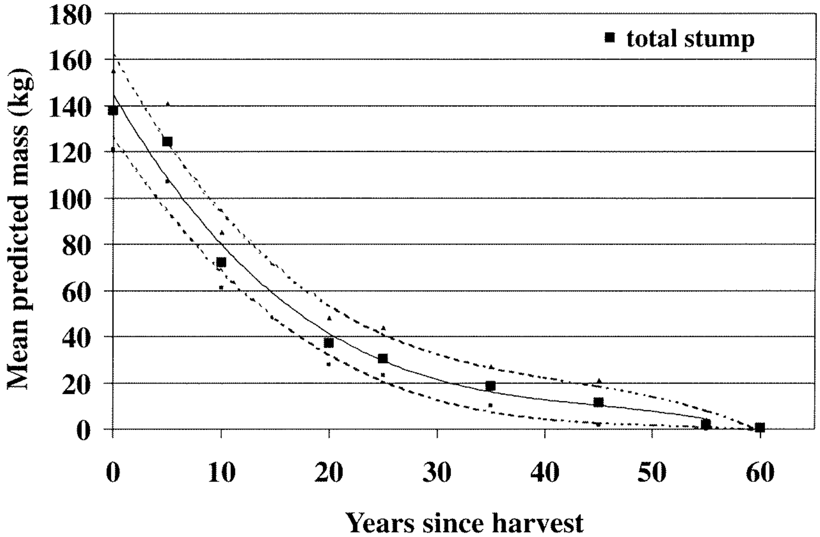
The strength of this decomposition model opens possibilities for improved estimates of the total resource pool and availability of carbon and other nutrients. It also provides researchers with a tool for quantifying carbon fluxes and spatial patterns of carbon cycling and nutrient pools in pine forests of the southeastern United States. The ability to relate lateral root diameters to an aboveground measure will further enhance our ability to predict spatial patterns of resource availability. These data support the important contribution of root systems to long-term resource availability. Evaluation of the relationship between stump diameters, years since harvest and decomposition should be tested un-

Table 3. Models for loblolly pine root decomposition by soil depth through 60 years since harvest.

Material	*a*	*b*	*c*	*d*	*r*	*P* >*F*
0–50 cm depth						
Total stump	78.409	0.327	0.164	–0.002	0.933	0.011
Total taproot	56.458	0.240	0.201	–0.002	0.946	0.009
Solid taproot	–186.960	6.065	–0.090	0.005	0.967	0.009
Soft taproot	–21.314	0.713	–0.001	0.0005	0.515	0.149
Lateral root	14.807	0.139	0.077	–0.000	0.688	0.085
Root bark	8.162	–0.071	0.113	–0.002	0.625	0.065
50–100 cm depth						
Total stump	–125.443	3.708	–0.157	0.006	0.852	0.045
Total taproot	24.895	–0.133	0.090	–0.001	0.654	0.074
Solid taproot	12.669	0.146	–0.086	0.002	0.651	0.115
Soft taproot	2583.923	–42.281	1.603	–0.026	0.814	0.217
Lateral root	–45.248	1.357	0.267	–0.003	0.879	0.081
Root bark	–7.795	0.201	–0.717	0.016	0.659	0.132

Note: The following model was used: total remaining mass (kg) = $(a + b(\mathrm{DIAM}))e^{(-c+d(\mathrm{DIAM}))\mathrm{YSH}}$.

Fig. 7. Confidence limits (95%) around the predicted mean of total loblolly pine stump biomass through 60 years, regressed against YSH and stump diameter, Durham, N.C., 2000.



der different management plans and on different soil drainage classes.

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References

Albaugh, T.J., Allen, H.L., Dougherty, P.M., Kress, L.W., and King, J.S. 1998. Leaf area and above- and belowground growth responses of loblolly pine to nutrient and water additions. For. Sci. **44**: 317–328.

Bloomfield, J., Vogt, K.A., and Vogt, D.J. 1993. Decomposition rate and substrate quality and foliage of two tropical tree species in the Luquillo Experimental Forest, Puerto Rico. Plant Soil, **150**: 233–245.

Chen, H., Harmon, M.E., and Griffiths, R.P. 2001. Decomposition and nitrogen release from decomposing woody roots in coniferous forests of the Pacific Northwest: a chronosequence approach. Can. J. For. Res. **31**: 246–260.

Cox, T.L., Harris, W.F., Ausmus, B.S., and Edwards, N.T. 1978. The role of roots in biogeochemical cycles in an eastern deciduous forest. Pedobiologia, **18**: 264–271.

Fahey, T.J., Hughes, J.W., Mou, P., and Arthur, M.A. 1988. Root decomposition and nutrient flux following whole-tree harvest of northern hardwood forest. For. Sci. **34**: 744–768.

Harris, W.F., Kinerson, R.S., and Edwards, N.T. 1977. Comparison of belowground biomass of natural deciduous forests and loblolly pine plantations. Pedobiologia, **17**: 369–381.

Jenny, H. 1980. The soil resource. Springer-Verlag, New York.

Joslin, J.D., and Henderson, G.S. 1987. Organic matter and nutrients associated with fine root turnover in a white oak stand. For. Sci. **33**: 330–346.

King, J.S., Allen, H.L., Dougherty, P.M., and Strain, B.R. 1997. Decomposition of roots in loblolly pine: effects of nutrient and water availability and root size class on mass loss and nutrient dynamics. Plant Soil, **195**: 171–184.

Nadelhoffer, K., and Raich, J.W. 1992. Fine root production estimates and belowground carbon allocation in forest ecosystems. Ecology, **73**: 1139–1147.

Olsen, J.S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology, **44**: 322–331.

Parresol, B.R. 2001. Additivity of nonlinear biomass equations. Can. J. For. Res. **31**: 865–878.

Pehl, C.E., Tuttle, C.L., Houser, J.N., and Moehring, D.M. 1984. Total biomass and nutrients of 25-year-old loblolly pine (*Pinus taeda* L.). For. Ecol. Manage. **9**: 155–160.

Raich, J.W., and Nadelhoffer, K.J. 1989. Belowground carbon allocation in forest ecosystems: global trends. Ecology, **70**: 1345–1354.

Richter, D.D., and Markewitz, D. 2001. Understanding soil change. Cambridge University Press, Cambridge, U.K.

SAS Institute Inc. 1985. SAS/STAT^{TM} guide for personal computers, version 6 ed. SAS Institute Inc., Cary, N.C.

U.S. Department of Agriculture (USDA). 2000. The 2000 RPA timber assessment update. USDA For. Serv. Gen. Tech. Rep. RM-259.

Van Lear, D.H., and Kapeluck, P.R. 1995. Above- and below-stump biomass and nutrient content of a mature loblolly pine plantation. Can. J. For. Res. **25**: 361–367.

Van Lear, D.H., Kapeluck, P.R., and Carroll, W.D. 2000. Productivity of loblolly pine as affected by decomposing root systems. For. Ecol. Manage. **138**: 435–443.

Vogt, K.A., and Persson, H. 1988. Root methods. *In* Ecophysiology of forest trees. Vol. 1. Techniques and methodologies. *Edited by* J.P. Lassoie and T.M. Hinckley. CRC Press, Boca Raton, Fla.

Vogt, K.A., Vogt D.J., and Bloomfield, J. 1991. Input of organic matter to the soil by tree roots. *In* Plant roots and their environment. *Edited by* B.L. Mcmichael and H. Persson. Development in Agriculture and Managed-Forest Ecology, Elsevier, Amsterdam. pp. 171–190.

Wells, C.G., Jorgensen, J.R., and Burnette, C.E. 1975. Biomass and mineral elements in a thinned loblolly pine plantation. USDA For. Serv. Res. Pap. SE-126.

Yavitt, J.B., and Fahey, T.J. 1982. Loss of mass and nutrient changes of decaying woody roots in lodgepole pine forests, southeastern Wyoming. Can. J. For. Res. **12**: 745–752.